THE DIOECIOUS AMARANTHS: A NEW SPECIES NAME AND MAJOR RANGE EXTENSIONS

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The ten dioecious species of *Amaranthus* (Amaranthaceae) are native pioneers of North American stream banks, lake shores, tidal marshes, and sea beaches. Except for the southern water-hemp, *A. australis,* which has a widely disjunct Gulf-Caribbean range attributable to waterfowl dispersal, all were originally confined to coherent, scarcely overlapping geographic ranges. During the last hundred years, several species have been expanding their ranges, mainly by gradual advances into adjacent territory as weeds of artificially modified habitats. Long-range seed dispersals have produced many isolated, ephemeral waifs but none of the species other than *A. australis* is known to have established successful disjunct colonies until very recently. This is in sharp contrast to the history of some monoecious species of *Amaranthus* that are notoriously successful as weedy colonizers and agrees with Baker's (1967) general rule that self-incompatible taxa are at a disadvantage in establishment after long-range dispersal.

A taxonomic revision of these species and a survey of their recent migrations were published about 15 years ago (Sauer, 1955, 1957). The present paper is intended as a supplement, presenting only information that is new or newly found since that time.

Rejection of Amaranthus tamariscinus Nutt.

This name and its synonyms, *Montelia tamariscina* (Nutt.) A. Gray and *Acnida tamariscina* (Nutt.) Wood, have long been applied to a species native to the southeastern Great Plains that has been gradually spreading northward and eastward since the mid 19th century. This species is clearly distinguished by the combination of dioecism, utricle dehiscence, and presence of a single well-developed tepal in the pistillate flowers. Unfortunately, as will be shown, Nuttall's name does not belong to this species, being based on a sterile hybrid between it and a monoecious species. It is obvious in retrospect that application of the name was based on habitat and geography rather than on diagnostic characters.

Nuttall (1835) published the name for plants he found in Arkansas Territory, in what is now Oklahoma:

> ". . . on the sand beaches of the Arkansas and Grand [Neosho] Rivers; abundant; possessing in some respect the aspect of *A. albus.* Stem 3–4 feet high and much branched, and as well as every other part of the plant perfectly smooth; flowering branches very compound and destitute of leaves, so as almost to resemble branches of *Tamarix gallicus,* the bracts being green, minute, imbricated and spinulose."

The description of the inflorescence, including the comparison with a tamarisk, has always been puzzling, being quite inappropriate for the species in question. Nevertheless, when the first collections of this species began arriving at Harvard, Gray bestowed Nuttall's name on them. Among the earliest were Drummond's *no. 240* from Texas in 1835 (GH) and Fendler's *no. 737* from Texas in 1846 (GH). Specimens grown at Harvard from seed of the latter in 1848 were sent to Kew labelled *Amaranthus tamariscinus* Nutt. in Gray's hand. Also a note from Gray to Hooker in 1876 is attached to a specimen of the former collection (K): "I have found my own specimen of No. 240, Drummond, Texas, which I can now certify to be the true 'Montelia tamariscina' i.e. Nuttall's plant—with circumscissile utricle. Vale." Gray was guessing about the utricle of Nuttall's plant. In his published treatment of the dioecious amaranths, Gray (1876) wrote: "Nuttall's specimens of this are not even in flower, so that he was unaware that the plant was dioecious and the fertile flowers achlamydeous." Later Uline and Bray (1895) reported that a fragment of Nuttall's type, then in the herbarium of Columbia College, was "very immature, but the locality, the slender, acuminate spikes, and the spinulose bracts enable us to determine its place with reasonable certainty." Like Gray, they identified it with the eastern Great Plains dioecious species and I made the same mistake (1955, 1957) until encountering a Nuttall specimen that I am convinced belongs to the type collection of *A. tamariscinus*.

This specimen is in the British Museum of Natural History and is labelled "Amaranthus *tamariscinus, Arkansas, Herb. T. Nuttall." The asterisk is Nuttall's standard indication of a new species. The inflorescence is in fact very compound and leafless and does strongly resemble a tamarisk. The plant is not at all immature but completely sterile and lacks even rudiments of flowers in the bract axils. It is an example of what Murray (1940) designated as neuter plants, bearing abundant bracts without flower primordia, which he produced in abundance in the course of an experimental investigation of sex determination among amaranths. These comprised a large proportion of the F_1 progeny of crosses between *"Acnida tamariscina"* and certain monoecious *Amaranthus* species. (For corrected determinations of some of Murray's experimental lines, see: Sauer, 1953.) Murray's voucher specimens (CU, F) of artificial hybrids between the eastern Great Plains dioecious species and *A. hybridus* L. are an excellent match for Nuttall's specimen. The native range of *A. hybridus* is mainly eastward of Oklahoma in moister parts of North America and southward into tropical America. It is interesting that it was already hybridizing with the local dioecious species before white settlement of the region. Later collections of these sterile hybrids are mostly from weed populations of artificially disturbed places rather than from river banks.

Nuttall also collected, perhaps at the same place, a normal specimen of the dioecious species; it has the typical simple inflorescence, unbranched

above the upper leaves. He labelled it "Amaranthus *virgatus, Arkansas" (BM) but unaccountably neglected to publish the name. Since the species has never been named, the following name is given.

Amaranthus rudis sp. nov.

Plantae annuae, dioeciae, caulibus erectis multiramosis, foliis oblongis. Inflorescentiae cymosae axillares et thyrsum longum terminale formantes. Bracteae 1½–2 mm longae, subulatae. Flores staminati pentameri, tepalis exterioribus circa 3 mm longis, acuminatis, tepalis interioribus circa 2½ mm longis, obtusis vel retusis. Flores pistillati tepalo evoluto unico circa 2 mm longo, acuminato; utriculus circumscisse dehiscens. Semen circa 1 mm diametro, nigrum.

TYPE: *J. B. Norton 428,* common weed, Riley County, Kansas, August 6, 1895. Holotype: Missouri Botanical Garden (MO 1740436). Isotypes: GH, KSC, NMC, RM, US.

Recent Dispersals of A. rudis

Isolated colonies of this species have continued to appear outside its coherent range, as they have since the late 19th century. However, the most recent finds are far more widespread than formerly and some of the isolated colonies are beginning to reproduce themselves.

The species was collected in 1970 at two places along the railroad near Charleston, West Virginia, the first records from the state. One was an unpollinated female (*O. L. Eye s.n.,* WVA) but the other included both sexes and was producing seed (*M. E. Denison s.n.,* WVA).

An old collection from the state of Washington was the sole record of the species west of the Rockies until 1957, when male and female plants were found ten miles apart along the railroad in Santa Barbara County, California (*H. M. Pollard s.n.,* CAS, LA). In 1969, a solitary male was found near the highway in a salt flat in Douglas County, Nevada (*J. T. Howell 46183,* CAS).

The first known record of any dioecious amaranth in Asia was a collection of both sexes of *A. rudis* on Okinawa in 1951 (*S. Sonohara s.n.,* KAG). The colony may be reproducing, since the species was collected on Okinawa again in 1955 (*T. Amano 7523,* KAG) and on nearby Toku no Shima in 1962 (*G. Ikeda 530,* KAG).

The first European record of the species (as "*A. tamariscinus*"), apart from a doubtful report from Hamburg in 1908, was from the Netherlands in 1953 (Aellen, 1961). A persistent colony has evidently been established near the harbor at Wageningen, where both males and seed-bearing females were collected in 1961 and subsequent years (*M. J. Jansen s.n.,* L, WIS). The same collections include sterile hybrids with *A. hybridus,* which preceded *A. rudis* to Europe by over a century. The two species have thus resumed in a Dutch urban habitat the miscegenation begun in the wilds of Oklahoma.

In England, male plants of this species are reported from the Avonmouth docks, Gloucestershire, in 1957 to 1959 (Brenan, 1961). In Czechoslovakia, the species was collected in 1967 and 1968 at three different railway yards and a river port, all in Northern Bohemia (*V. Jehlík 4052–4056,* WIS). Both sexes were represented but no seed was borne on the specimens examined.

Adventive A. Arenicola in California

Amaranthus arenicola I. M. Johnston is native to the High Plains and was not recorded west of the Rockies until 1963, when it was reported at two places in California (Howell, 1966). Collections consist of an immature female found by the railroad at Santa Barbara (*H. M. Pollard s.n.,* CAS) and part of a large, isolated female bearing a few presumably hybrid seeds that was found near the highway at King City, Monterey County (*J. T. Howell 4066,* CAS). Although an annual at home, the species can live longer in California. Howell found the same Monterey County plant flourishing over a year later, but it has since disappeared. In 1965 *A. arenicola* was collected along the highway near Santa Ynez in Santa Barbara County, about 25 miles from the previous Santa Barbara record; the colony extended for some distance along both sides of the road and included both sexes (*C. F. Smith 9065,* CAS). By 1971 the same colony numbered thousands of plants, mostly right at the edge of the road shoulder (*J. Sauer 4871,* LA, WIS); the plants face immediate bulldozing in a massive highway reconstruction project but this may cause further dissemination.

Recent Dispersals of A. palmeri

Amaranthus palmeri S. Wats. has been by far the most successful field weed of all the dioecious amaranths. Native to Mexico and the southwestern United States, it has been expanding its range on various borders since 1900. It has been found in five additional states since 1960, all north and east of its former range. In 1962 in the first Arkansas record, it was found in cotton fields around Newport as a conspicuous weed that was producing abundant seed (*J. Sauer & D. Gade 3358,* B, F, DAV, WIS). Another colony was found in 1963 near Malvern, Arkansas, on a site disturbed by road work (*D. Demaree 48940,* WIS). In Nebraska in 1963, a troublesome new weed, 10 to 12 feet tall, was reported interfering with mechanical corn pickers near Trenton; subsequently a mass collection (*J. Furrier s.n.,* WIS) showed these giants to be sterile hybrids in mixed populations of *A. rudis* and newly immigrated *A. palmeri.* In the first South Carolina record, seed-bearing *A. palmeri* was collected in a cornfield near Sumter in 1966 (*T. Bradley & R. S. Blaisdell 3443,* U, WIS). The species first appeared in Florida in 1967, already producing seed, near Immokalee (*D. B. Ward s.n.,* WIS). The

species was first found in West Virgnia in 1970 along the railroad near Charleston; the specimen is an immature female (*M. E. Denison s.n.,* WVA). The first known Canadian record, also pistillate and seedless, was a garden weed at Lambton, Ontario, in 1963 (*L. Gaiser s.n.,* WIS).

The earliest European collections of *A. palmeri* were from cotton mill waste in Bohemia in 1908 (*V. V. Cypers s.n.,* W) and Switzerland in 1921 (*R. Probst s.n.,* L); only staminate plants were included. There were few more finds until the 1950's, when they began to multiply. The total is now over 25, almost all from cotton mill waste or other dumps or dock areas. These will not be cited in detail because they do not represent established colonies. Both sexes occur but no seed-bearing specimens are known. However, it is remarkable how widely the species has been found: Sweden (W), England (L, WIS), Netherlands (L, U, WIS), Luxembourg (WIS), Germany (K, M, W, WIS), and Austria (W). Aellen (1961) and Brenan (1961) cite additional collections that I have not seen. Seed of *A. palmeri* must be arriving continually in cotton bales from the United States, maybe more frequently since picking was mechanized. The rate may also have increased with the recent immigration of the species into cotton fields of the southeastern states and perhaps even more with expansion of cotton growing in the western states where it is a native. Twisselmann (1963) noted that *A. palmeri* had become a common and widespread weed in San Joaquin valley cotton fields.

European Colonies of Other Species

Although native to the Midwestern United States, *Amaranthus tuberculatus* (Moq.) Sauer was originally described in 1849 from living plants in the Geneva Botanical Garden; both sexes were present and producing seed. The species was also being grown at the Munich Botanical Garden between 1849 and 1853 (*Anonymous s.n.,* M). A hundred year gap in the record ensues before the species reappears as a weed. Since 1949, both sexes have been found repeatedly along railroads and on dumps near Graz, Austria (*H. Melzer s.n.,* WIS; other citations by Aellen, 1961). In 1958 and 1959, individual female plants were found on the Avonmouth docks where *A. rudis* and *A. palmeri* were also found (Brenan, 1961).

Another dioecious amaranth, *A. watsonii Standl.,* was also collected on the Avonmouth docks in 1959, both sexes being present (Brenan, 1961). This species is native to arroyos and beaches of Baja California but may have arrived via southern California, where it has been spreading as a weed since about 1900.

Range Extensions of A. australis

Amaranthus australis (A. Gray) Sauer, the southern water hemp, has extensive populations in the Everglades and the Gulf coast of the south-

ern United States. Widely scattered colonies have long been known from a few places in Mexico, the West Indies, and Venezuela. Some additional disjunct colonies, none of which appear to be new, can now be reported.

In 1962, a large population of *A. australis* was found near Chenkán, Campeche, Mexico, growing with sedges and cattails in a marsh behind the coastal beach ridges (*J. Sauer & D. Gade 3183,* F, WIS). The nearest previously known colonies lie 150 miles to the southwest in Tabasco and 250 miles to the northeast in Quintana Roo.

Until recently, I was unaware that the species ranged into the Guianas. European herbaria have many specimens from Surinam, the earliest collected in 1920 at the mouth of the Corantijne River (*A. Pulle 376,* U; *378,* BM, K). Twelve other Surinam collections were made between 1927 and 1969 in the districts of Nickerie, Coronie, Saramacca, Suriname, and Marowijne (K, U). Notations on these show that the plant is common in coastal marshes, both fresh and brackish, and on margins of mangrove swamps. As in the Everglades, the plants reach giant size; notes on Surinam specimens (U) give plant heights up to 5 m, stem diameters to 25 cm. The species is also reported as common in coastal sedge-cattail marshes in western French Guiana; a synonymous name is used: *Acnida cuspidata* (Vann, 1969).

From Brazil, I have seen only one collection, a seed-bearing female found near Porto Alegre, Rio Grande do Sul, in 1899 (*E. M. Reineck s.n.,* E). This is some 2,500 miles from the nearest Guiana collections, but unknown colonies may exist in the intervening swamps and marshes.

There is some new evidence that migratory birds may disperse amaranth seeds over long distances, although it does not derive specifically from *A. australis*. DeVlaming and Proctor (1968) reported that *Amaranthus* and *Polygonum* seeds, unidentified as to species, often constitute the bulk of the seeds in the digestive tracts of killdeer shot in Texas. They fed *A. palmeri* seeds to captive killdeer and mallard ducks and found that they were passed in viable condition after many hours retention within the bird, long enough for killdeer to fly over 1,000 miles and mallards over 500.

Distribution of A. greggii Clarified

Amaranthus greggi S. Wats. appeared in my revision (1955) as a rare species, known from only 3 Texas and 6 Mexican localities. The distribution is now much better known (fig. 1). The following citations, located by municipio, parish, or county within each state, should be added to those given previously. The additional citations all date from between 1958 and 1965 except Wawra's. Heinrich Wawra, Ritter von Fernsee, was chief surgeon on the Austrian frigate "Novara" on which Maximilian and Carlotta sailed to claim their Mexican empire in 1864.

The ship is known to have made a brief excursion around the Gulf while stationed at Vera Cruz the following year and Wawra's collections were probably made then.

Abbreviations: *J. S(auer); D. G(ade).*

Mexico

CAMPECHE. CAMPECHE: *J. S. 2412,* B, BM, F, GH, MICH, MO, UC, WIS. CARMEN: *J. S. 2446,* F, WIS; *J. S. & D. G. 3148,* WIS; *3352,* WIS; *H. Wawra 235,* W. TABASCO. FRONTERA: *J. S. & D. G. 3117,* DAV, WIS, *3142,* WIS. PARAISO: *F. Barlow* 12/6, WIS. TAMAULIPAS. VILLA CECILIA: *J. S. & D. G.*

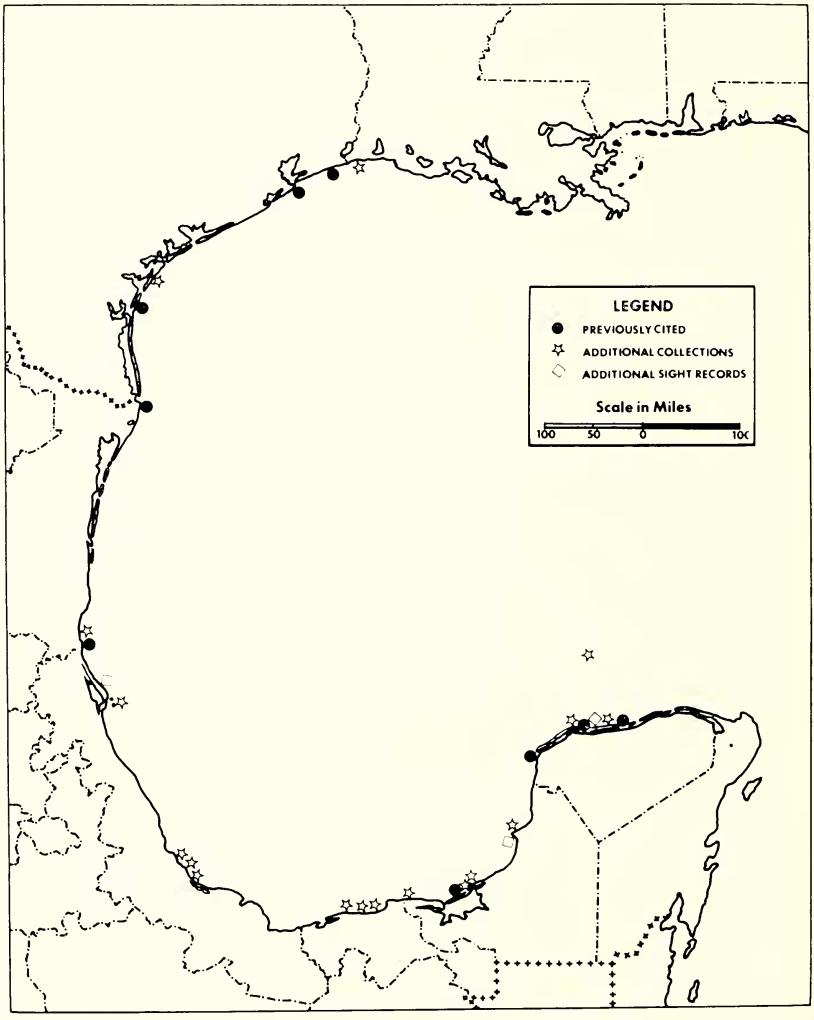

FIG. 1. *Amaranthus greggii:* revised distribution map.

2960, F, WIS. VERA CRUZ. ALVARADO: *J. S. & —D. G. 3102,* WIS; *H. Wawra 431,* W. BOCA DEL RIO: *J. S. 2465,* F, WIS: *J. S. & D. G. 3085,* WIS. TAMIAHUA: *W. G. McIntire s.n.,* WIS. YUCATAN. ARRECIFE ALACRAN: *H. Wawra* 106, W. DZILAM: *J. S. & D. G. 3225,* WIS. PROGRESO: *J. S. 2360,* BM, DH, F, GH, MICH, MO, UC, WIS.

United States

LOUISIANA. CAMERON: *J. W. Thieret & W. D. Reese 10028,* WIS. TEXAS. ARANSAS: *J. S. 2572,* WIS, *2607,* TEX.

Sight records (fig. 1) are from published vegetational transects (Poggie, 1962; Sauer, 1967).

Amaranthus greggii has an extraordinarily predictable distribution pattern. Its niche is a linear zone at the outer fringe of pioneer beach vegetation; it commonly grows closer to the sea than any other species. It is relatively indifferent to grand regional rainfall gradients. It does not grow on limestone shores or other stable substrates but only on loose sand. The sand may be light or dark, calcareous, quartz, or of heavy minerals. It makes little difference whether the beach is wild and remote or inhabited and heavily trodden. The species is particularly abundant at the head of the Bay of Campeche and along the northern Yucatan barrier islands; in both sectors it is a summer colonizer of beaches swept clean by northerly winter storm winds, the famous Gulf *nortes.* Its frequency decreases northward along the Vera Cruz coast. On the Tamaulipas and Texas barrier islands there seems to be no regular niche for it between the bare beach and the grassy foredunes. In this sector, sporadic occurrences may increase after hurricanes. For example, in 1959 near Port Aransas, Texas, I found only a few isolated individuals of the species on St. Joseph and Mustang Island beaches, none at all in rather extensive transects of the dunes. In the same area in 1962, nine months after hurricane Carla, *A. greggii* was conspicuous and locally abundant in the devastated dunes. Thieret and Reese's outlying Louisiana record was also made the year after Carla and was probably ephemeral.

Presumably seeds are continually floating up the Tamaulipas and Texas coast in the predominantly clockwise longshore currents from the tropical stronghold of the species. The seeds alone are not buoyant but the indehiscent, inflated utricles are and I have found they float in an occasionally agitated Petri dish for over a week before waterlogging.

It seems likely that *A. greggii* evolved into a distinct species along the tropical Gulf coast beyond the range of *A. arenicola,* its closest relative. Evolutionary changes required to derive *A. greggii* from the latter consist of little more than suppression of utricle dehiscence and increasing coriacous texture of the foliage. Although its main populations are in the High Plains, *A. arenicola* approaches the Gulf in southern Texas and Tamaulipas. At the mouth of the Rio Panuco, it grows on active dunes (*J. S. & D. G. 2959,* F, WIS) within sight of storm beach colonies of *A. greggii.* Apparent hybrids occur, including the types of *A. myrian-*

thus Standl., collected at the mouth of the Rio Panuco in 1910 (*E. Palmer 266, 511,* CAS, GH, K, MO, US, WIS).

The peculiarly regular winter storm regime of the Gulf evidently offered an evolutionary opportunity for an annual pioneer from a temperate zone background. *Amaranthus greggii* and a few of its associates, e.g. species of *Cakile,* are anomalous in this respect among the mass of tropical beach pioneers, which are typically perennials adapted to nonperiodic storm regimes.

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